Biological Journal of the Linnean Society, 14: 103–131. With 2 figures
August 1980

Food, feeding ecology and ecological segregation of seabirds at South Georgia

J. P. CROXALL AND P. A. PRINCE

Life Sciences Division, British Antarctic Survey, Natural Environment Research Council, Madingley Road, Cambridge CB3 0ET, England

Accepted for publication January 1980

At the sub-Antarctic island of South Georgia 25 of the 29 breeding species are seabirds. Fifteen of these have recently been studied in some detail. By examining the timing of their breeding seasons and their diet and feeding ecology (especially feeding techniques and potential foraging ranges), the nature of their ecological isolating mechanisms, and in particular the way in which they partition the resources of the marine environment, are reviewed.

Although breeding season adaptations occur (winter breeding in Wandering Albatross and King Penguin; out of phase breeding in two species-pairs of small petrels) these are less important than differences in food and feeding ecology. There is a fundamental distinction between the niche of pursuit-diving species (mainly penguins) and the remainder which are basically surface-feeders. The two abundant krill-eating penguins show clear differences in feeding zones. Three albatrosses and a petrel feed mainly on squid and there are differences in both the species and size of the prey of each. The remaining seabirds chiefly take krill (although the giant petrels are extensive scavengers and some smaller petrels specialize on copepods) and utilize different feeding methods and areas to do so.

Various adaptations related to inshore and offshore feeding zones are discussed. Although most species possess a combination of ecological isolating mechanisms additional evidence for the particular importance of dietary differences is presented.

CONTENTS

0024–4066/80/050103 + 29$02.00/0

INTRODUCTION

While the nature of ecological isolating mechanisms operating in multi-species seabird communities has received some attention in north temperate and tropical regions (e.g. Belopolskii, 1957; Ashmole & Ashmole, 1967; Ashmole, 1968; Pearson, 1968; Cody, 1973) there has been no similar detailed investigation of any south temperate, sub-Antarctic or Antarctic situation although Carrick & Ingham (1967, 1970) summarized much general information for Antarctic areas.

The southern oceans, particularly in the last two regions, are well known to be rich in plant and animal plankton and nekton and to support an extensive array of vertebrate predators including vast numbers of seabirds. At high latitudes, such as the periphery of the Antarctic continent, the exceptional seabird biomass is not matched by a comparable species diversity. At the sub-Antarctic islands, however, most of the considerable diversity of seabird species are present in substantial numbers. This circumstance is probably due to a combination of the rich upwelling areas around the islands' continental shelves and their proximity to the highly productive area of water mixing known as the Antarctic Convergence and to the very restricted amount of suitable land areas for breeding in these latitudes.

Although South Georgia is a little further south than the other islands usually classified as sub-Antarctic (e.g. Prince Edward Islands, Crozet Islands, Kerguelen Island, Macquarie Island) it still lies only 300 km south of the Antarctic Convergence. Of its 29 species of breeding birds (Prince & Payne, 1979) there are 16 procellariforms (albatrosses, petrels etc.) five penguins and four other species (shag, skua, gull and tern) which derive all or part of their food from the sea.

In the last few years the biology and ecology of many of the albatrosses, petrels and penguins have been studied at Bird Island (a small island of *c.* 500 ha off extreme north-west South Georgia) usually with particular emphasis on diet and feeding ecology. Although much of the research is still in progress this would seem a useful stage to summarize our present ideas on the morphological, behavioural, ecological and temporal mechanisms by which these species partition the resources of the surrounding marine environment.

SPECIES

A list of the main species to be discussed and an estimate of the size of their current breeding population at South Georgia and Bird Island is given in Table 1; selected measurements of these species appear in Appendix 1 and 2.

The Table, and most of what follows, is confined to procellariforms and penguins. We have only anecdotal information on the four species thus excluded; three (shag, gull and tern) breed only in very small numbers on Bird Island and all four appear to have very distinct ecological roles, each typical of its group, which overlap hardly at all either with each other or with the other seabirds. The Antarctic Tern feeds very close inshore, usually in sheltered water, by contact dipping (picking prey from the sea surface while momentarily halting flight) or shallow plunging; Southern Black-backed Gull feeds mainly on marine organisms in the intertidal zone or close inshore waters; the Brown Skua is part scavenger (at fur seal and penguin colonies), part predator of small petrels, mainly at night; Blue-eyed Shag is chiefly piscivorous in water close inshore,

Table 1. Estimated breeding population size (pairs) of seabirds at South Georgia and Bird Island

	Species	South Georgia	Bird Island	Reference
King Penguin	*Aptenodytes patagonica* J. F. Miller	22,000	–	Smith & Tallowin, 1980
Chinstrap Penguin	*Pygoscelis antarctica* (Forster)	2000 +	10	Prince & Payne, 1979
Gentoo Penguin	*Pygoscelis papua* (Forster)	c. 100,000	1200–6500	Croxall & Prince, 1979
Rockhopper Penguin	*Eudyptes crestatus* (J. F. Miller)	10–50	1–2	Prince & Payne, 1979
Macaroni Penguin	*Eudyptes chrysolophus* (Brandt)	5 million +	175,000	Croxall & Prince, 1979
Wandering Albatross	*Diomedea exulans* L.	4300	2600	Croxall, 1979
Black-browed Albatross	*Diomedea melanophris* Temminck	60,000	12,600	Prince & Payne, 1979
Grey-headed Albatross	*Diomedea chrysostoma* Forster	60,000	14,500	Prince & Payne, 1979
Light-mantled Sooty Albatross	*Phoebetria palpebrata* (Forster)	8000–13,000	150	–
Southern Giant Petrel	*Macronectes giganteus* (Gmelin)	20,000–30,000	600	S. Hunter, 1979
Northern Giant Petrel	*Macronectes halli* (Mathews)	5 000–15,000	1100	S. Hunter, 1979
Cape Pigeon	*Daption capense* (L.)	1000–5000	100	Prince & Payne, 1979
Snow Petrel	*Pagodroma nivea* (Forster)	1000–5000	2	
Dove Prion	*Pachyptila desolata* (Gmelin)	millions	500,000 +	
Blue Petrel	*Halobaena caerulea* (Gmelin)	50,000–100,000	10,000 +	
White-chinned Petrel	*Procellaria aequinoctialis* (L.)	20,000–60,000	5000 +	
Wilson's Storm Petrel	*Oceanites oceanicus* (Kuhl)	100,000 +	2000 +	
Black-bellied Storm Petrel	*Fregetta tropica* (Gould)	scarce	100 +	
Grey-backed Storm Petrel	*Garrodia nereis* (Gould)	scarce	?	
South Georgia Diving Petrel	*Pelecanoides georgicus* Murphy & Harper	100,000 +	5000	
Common Diving Petrel	*Pelecanoides urinatrix exsul* Salvin	50,000 +	5000 +	
Blue-eyed Shag	*Phalacrocorax atriceps* King	2000–5000	100	
Brown Skua	*Catharacta lonnbergii* (Mathews)	2000–5000	350	
Southern Black-backed Gull	*Larus dominicanus* Lichtenstein	500–1000	20	
Antarctic Tern	*Sterna vittata* Gmelin	1000 +	25	

Figures without reference are based on the current information in B.A.S. files. They will be fairly accurate for !Bird Island, less so for South Georgia.

particularly around kelp beds although the population at Shag Rocks, 200 km west of South Georgia, must be considerably more oceanic in habit. These species will not be treated subsequently except where their ecological role appears relevant to the remaining species.

Table 1 shows also that there are six other species (Chinstrap and Rockhopper Penguins, Snow and Cape Petrels, Black-bellied and Grey-backed Storm Petrels) that are at best scarce breeding species at South Georgia. Except for Chinstrap Penguin we have little information even on their diet. Attention will therefore be focussed chiefly on the remaining 15 species, comprising three penguins, four albatrosses, five petrels, two diving petrels and a storm petrel.

BREEDING HABITAT

The existence of nest site preferences has been well described for northern hemisphere auks (e.g. Lack, 1934; Sergeant, 1951) and noted for other seabirds. Together with evidence for interspecific competition for nest sites (e.g. Belopolskii, 1957; Bedard, 1959a) such habitat segregation has been recognized as a significant ecological isolating mechanism, at least in situations where available breeding sites are in limited supply.

Some South Georgia seabirds show distinct habitat preferences when breeding and these are summarized, together with information on the nature of their breeding aggregations, in Table 2. The ubiquity of the tussock grass *Poa flabellata* (Lam.) Hook. f. habitat, the dominant vegetation type, and its suitability as a substrate for burrowing petrels ensures that most species breed in this habitat. With the petrels and particularly the two diving petrels (see Payne & Prince, 1979, for full details) it is possible often to recognize certain preferences of aspect, slope and microhabitat (cf. Richdale, 1965) and these are being investigated at Bird Island while census work on the burrow-dwelling species is in progress.

With no species has any form of interspecific nest site competition been observed. For all species there appear to be available extensive areas of fully suitable breeding habitat as yet unexploited and it is very difficult to believe that nest site availability has any significant effect on breeding population numbers. It is particularly notable that few species at South Georgia breed on cliffs. The absence of predators may be responsible for this contrast with the northern hemisphere where cliff nesting is such a feature of seabird biology.

There seem to be no obvious disadvantages attending the choice of particular breeding habitats as even the most inland sites are seldom more than a few hundred metres from the sea and most species-specific differences in site topography are probably interpretable in relation to species' morphological, behavioural and ecological adaptations.

TIMING OF BREEDING SEASON

Most South Georgia seabird species show very high synchrony of breeding events both within and between seasons. Egg laying is usually completed within two to three weeks and variation in laying date from season to season is often much less than this. This is not true for King Penguin (discussed in detail below), nor for Gentoo Penguin where, although each colony is fairly well synchronized, there may be considerable intercolony variation and a four to five week season to

Table 2. Breeding habitat and dispersion of South Georgia seabirds

Species	Breeding sites	Breeding dispersion and size	Inter-nest distance
King Penguin	flat beaches	usually large colonies (10^3)	1 m
Chinstrap Penguin	beaches, slopes	medium colonies (10^2–10^3)	0.75 m
Gentoo Penguin	flat beaches, tussock	small colonies (10^2)	1 m
Macaroni Penguin	steep coastal slopes	very large colonies (10^4+)	0.5 m
Wandering Albatross	tussock flats	loose aggregations	10–20 m
Grey-headed Albatross	tussock slopes	medium colonies (10^2–10^3)	1–2 m
Black-browed Albatross	steep tussock slopes	medium colonies (10^2–10^3)	1–2 m
Light-mantled Sooty Albatross	tussock cliffs	solitary-small groups (< 10)	5–10 m
Southern Giant Petrel	tussock flats	loose aggregations	5–10 m
Northern Giant Petrel	tussock flats (often coastal)	loose aggregations	5–10m
Cape Pigeon	ledges of coastal cliffs	small groups	–
Snow Petrel	crevices of high (300 m a.s.l.) inland cliffs	small groups	–
Dove Prion	tussock flats, slopes	dense colonies	1400/1000 m^2
Blue Petrel	tussock flats, slopes	locally dense colonies	720/1000 m^2
White-chinned Petrel	tussock ridges, hills, slopes	locally dense colonies	40/1000 m^2
Wilson's Storm Petrel	coarse scree, rubble, cliff crevices	medium colonies (10^2–10^3+)	
South Georgia Diving Petrel	fine, high (100–250 m a.s.l.) scree	small colonies (10^2)	200/1000 m^2
Common Diving Petrel	very steep coastal tussock slopes	local medium colonies (10^2–10^3)	

For burrow-dwelling species (below horizontal line) values are breeding densities (occupied burrows/1000m^2) for optimum habitats (data from I. Hunter (1979) and pers. comm.).

season variation in laying date has been recorded. The storm petrels are probably also poorly synchronized, as at Signy Island (Beck, 1970), but there are insufficient data.

The average duration of the breeding season, from egg-laying to chick fledging, of South Georgia penguins and petrels is shown in Fig. 1. This shows clearly that for most species the onset of breeding is October–November with fledging February–March–April. The relative consistency of this pattern is, of course, a reflection of the strong seasonality of the environment with phytoplankton production virtually restricted to the period October–May with a single pronounced peak in the South Georgia area around early December (Hart, 1942) and mean zooplankton biomass in the 0–50 m depth zone rising steadily from October to a peak in April and returning to very low levels by July (Foxton, 1956; 1964).

In general terms the larger seabirds (e.g. albatrosses, giant petrels), with

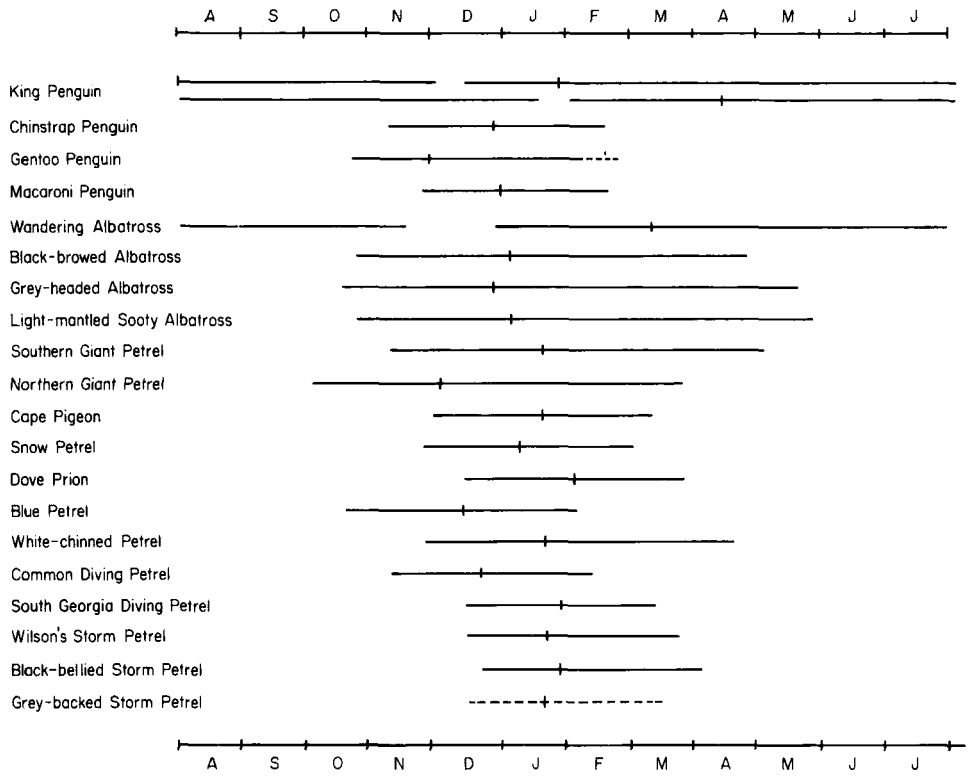

Figure 1. Breeding seasons of South Georgia seabirds. Horizontal lines run from mean laying to mean fledging date. Vertical bar is mean hatching date. Broken line indicates dates or period uncertain.

inevitably longer incubation and fledging periods, appear to commence breeding as soon as practicable (usually in October) apparently in order to ensure that chicks are fledged while rich supplies of zooplankton remain available. For smaller seabirds, with a shorter breeding season, it is clearly possible for its onset to be considerably delayed and fledging at an optimum period maintained.

In spite of the considerable similarities referred to there are two anomalous species and several other features of particular interest. At South Georgia Stonehouse (1960) found that breeding King Penguins usually follow a sequence of early breeding (laying in November–December, chick fledging following November), late breeding (laying February–April, chicks fledging January–February) and non-breeding in three successive seasons, raising, at best, two chicks in this period. At Iles Crozet a somewhat similar situation prevails, although it appears that birds there may only breed successfully in alternate seasons (Barrat, 1976).

It has been suggested (Stonehouse, 1960) that this system has been adopted due to the inability of King Penguins to lay eggs before November which thus prevents chicks being fledged before June (at a time when food resources are dwindling to a minimum). The chicks are therefore sustained with sporadic feeds through the winter and fledge in early summer when food is plentiful; the parents can then return to breeding condition and lay in late summer but this

chick, if it survives the high winter mortality, does not fledge until mid-summer and the parents are now unable to commence breeding again that season.

Similar arguments (long chick fledging period in relation to resource availability) can be advanced to account for the Wandering Albatross rearing its chick with regular feeds throughout the winter. The chicks fledge in late November and adults that successfully raise a chick (and those that lose it after June) can only breed biennially (Tickell, 1968). In this context it should be noted that such greater than annual breeding periodicity is not associated solely with winter breeding species; Grey-headed and Light-mantled Sooty Albatrosses are both biennial breeders when successful (Tickell & Pinder, 1967; Prince, unpublished data; Kerry, pers. comm. and in prep.).

The flexibility in timing of breeding season available to the smaller petrels has already been mentioned. In two cases it appears that this may have been used to reduce interspecific competition, particularly with respect to the time of greatest demands for food, i.e. when raising chicks. Thus, both for Dove Prion and Blue Petrel and for South Georgia and Common Diving Petrels, chick-rearing periods are virtually mutually exclusive.

Unfortunately, there are no data on timing of the breeding season for sites at which only one member of these 'species-pairs' breed, to indicate if an alternative breeding schedule is possible. At Signy Island, in the absence of Blue Petrel, Dove Prion commences breeding at a date similar to that on South Georgia (Tickell, 1960). However Signy Island is much further south and breeding probably starts as early as conditions permit (Beck, 1970). Other subspecies of Common Diving Petrel in the New Zealand area are likewise early breeders (Richdale, 1965; Thoresen, 1969) but there are several small petrels (though no other diving petrel) that breed later. While the staggered breeding seasons of the two sibling species of giant petrels, which consistently lay about six weeks apart, may chiefly function as a reproductive isolating mechanism (and even so hybrid pairs are occasionally reported (Burger, 1978; S. Hunter, 1979) it will be seen that this may also play a part in restricting the extent of direct competition for food.

DIET

A summary of the results of quantitative studies on the diet of South Georgia seabirds is presented in Table 3. Also included are estimates derived from earlier qualitative analyses where these have been confirmed by current observations. Data obtained farther south have been used for three species as our observations indicate that a similar situation prevails at South Georgia, where we lack fully quantitative information.

More comprehensive information can be found in the references indicated, in most of which details of the frequency of occurrence and number of individuals in each prey class are given. For the present purpose the weight data were thought to provide the most straightforward and relevant picture. Details of the various sampling and analytical techniques employed are given, principally in Prince (1980 a, b) and Croxall & Prince (1980). In particular it should be noted that most samples were obtained from adults just about to feed their chicks, thus avoiding the problems of food accumulation that result if samples are taken from chicks.

Table 3. Percentage composition by weight of diet of South Georgia seabirds

Species	Main prey classes					Crustacean prey				Reference
	Squid	Fish	Lamprey	Crustacea	Carrion	Euphausiids	Decapods	Amphipods	Copepods	
King Penguin	(90)	(10)		+						unpublished data
Chinstrap Penguin		4**		96**		100**		+		Croxall & Furse, 1980
Gentoo Penguin		32		68		100		+		Croxall & Prince, 1980
Macaroni Penguin		2		98		100		+		Croxall & Prince, 1980
Wandering Albatross	(80)	(10)		(+)	(+)					Tickell, 1968; Clarke *et al.*, in press
Black-browed Albatross	21	38	1	40	+	95	2.5	2.5		Prince, 1980b
Grey-headed Albatross	49	24	11	16		96	2	2		Prince, 1980b
Light-mantled Sooty Albatross	47	11		41	+	89	10	1		Thomas, unpublished data
Southern Giant Petrel	(10)			(50)	(40)	(100)				S. Hunter, unpublished data
Northern Giant Petrel				(30)	(70)	(100)				S. Hunter, unpublished data
Cape Pigeon		(15)*		(80)*	+	(80)*		(12)*	+	Beck, 1969
Dove Prion	1	2		97		60		8	32	Prince, 1980a
Blue Petrel	1	8		91		90	1	5	4	Prince, 1980a
White-chinned Petrel	47	24		80		96	2	2		Prince, unpublished data
Wilson's Storm Petrel				(95)*		(95)*		+		Beck, 1972
South Georgia Diving Petrel				100		15		17	68	Payne & Prince, 1979
Common Diving Petrel				100		76		4	20	Payne & Prince, 1979

* Data for Signy Island, South Orkney Islands.
** Data for Elephant Island group, South Shetland Islands.
() Values derived from qualitative analysis.
\+ Present in small quantities.

The basic breakdown of consumers in respect of the major prey classes can now briefly be summarized before the further segregation that may be achieved by feeding ecology is considered.

Fish

Fish are taken by many species in the Table but are the principal prey of none, although they almost certainly predominate in the diet of Blue-eyed Shag. Fish are important in the diet of Black-browed Albatross, Grey-headed Albatross, Gentoo Penguin and White-chinned Petrel and also for Blue Petrel. This last is not apparent from the table but Prince (1980a) noted that fish occurred in 83% of samples and if the components of the highly digested totally unidentifiable material are (reasonably) attributed to fish then they would contribute 50% by weight to the diet and the crustacean contribution would be commensurately reduced.

Except in Gentoo Penguin, the condition of fish material has usually been insufficient for identification, other than at the family level of Myctophidae and Notothenidae and *Pseudochaenichthys georgianus* Norman (Chaenichthyidae) in some albatross samples. In the Gentoo Penguin material specimens of *Notothenia rossii* Richardson, *N. larseni* Lonnberg and *Champsocephalus gunnari* Lonnberg *c.* 25 cm long were identified (Croxall & Prince, 1980); *N. gibberifrons* Lonnberg 9–12 cm long has been recorded in a stomach examined at Signy Island (Conroy & Twelves, 1972). Blue Petrels take very small fish (and probably mainly myctophids) but it is not possible to discern any differences between the fish portion of the diet in the other species.

The presence of lampreys in the diet of Grey-headed Albatross (and hardly at all in Black-browed Albatross) is particularly noteworthy. The specimens were nearly mature individuals, probably just about to return to their South American breeding rivers (Potter, Prince & Croxall, 1979), of *Geotria australis* Gray, a species only recorded hitherto in the diet of one other seabird, Black Petrel *Procellaria parkinsoni* Gray (Imber, 1976).

Squid

Squid appear fundamental to the diet of King Penguin and Wandering Albatross and very important as a food for Grey-headed Albatross, Light-mantled Sooty Albatross and White-chinned Petrel.

While we have no squid material for King Penguin and that for White-chinned Petrel is still being analysed it is possible to compare in more detail the composition of the squid portion of the diet of four albatrosses (the three mentioned above plus Black-browed Albatross) in Table 4. This table includes details of all squid species which formed more than 5% by numbers or weight of the squid diet of any of the albatrosses.

Some clear differences are apparent. Many squid species were recorded from Wandering Albatross but the bulk of its diet is made up by *Kondakovia longimana* of mean weight just over 3 kg. Grey-headed and Black-browed Albatrosses mainly took *Todarodes sagittatus* of mean weight just under 200 g. *Mesonychoteuthis* species (mean weight 80 g) was the most abundant squid in Light-mantled Sooty Albatross samples but *Discoteuthis* (mean weight *c.* 700 g) made up the bulk by weight. It would seem therefore that, with the exception of the very similar (in

Table 4. Composition of squid component of albatross diets

	Wandering Albatross ($N = 534$) %			Grey-headed Albatross ($N = 190$) %			Black-browed Albatross ($N = 97$) %			Light-mantled Sooty Albatross ($N = 191$) %		
	No	Wt	Mean Wt (g)	No	Wt	Mean Wt (g)	No	Wt	Mean Wt (g)	No	Wt	Mean Wt (g)
Cranchidae												
Mesonychoteuthis sp. A	5	<1	84	12	5	74	25	13	81	56	17	81
Taonius pavo Lesueur	5	6	319	–	–		–	–		–	–	
Crystalloteuthis sp.	15	3	276	–	–		–	–		2	1	*c.* 270
Onychoteuthidae												
Kondakovia longimana Filippova	36	78	3170	–	–		1	1	203	<1	2	*c.* 1000
Histioteuthidae												
Histioteuthis ? eltaninae (Voss)	10	<1	71	–	–		–	–		<1	<1	*c.* 70
H. atlantica (Hoyle)	3	1	192	–	–		–	–		–	–	
Gonatidae												
Gonatus antarcticus Lonnberg	4	1	330	–	–		–	–	186	5	6	*c.* 300
Gonatus sp.	2	<1	162	–	–		–	–		8	5	*c.* 150
Cycloteuthidae												
Discoteuthis sp.	–	–		–	–		–	–		21	60	726
Octopoteuthidae												
Taningia danae Joubin	2	8	6520	–	–		–	–		–	–	
Enoploteuthidae												
Ancistrocheirus lesueuri (d'Orbigny)	2	2	1476	–	–		1	7	1110	–	–	
Psychroteuthidae												
Psychroteuthis sp.	–	–		–	–		–	–		5	9	570
Ommastrephidae												
Todarodes sagittatus (Lam.)	1	<1	350	84	95	183	67	76	189	2	<1	*c.* 180
Other species	(14) 11	<2		(1) 4	<1		(1) 3	2		(1) <1	<1	

1. Number of additional species is in parenthesis on bottom row of table.
2. References: Clarke *et al.*, in press; Prince, 1980b; Clarke & Prince, in press; unpublished data.

body and bill dimensions) Grey-headed Albatross and Black-browed Albatross (and squid is of small importance in the diet of the latter) the albatrosses take squid of both different species and sizes. There are, however, differences in the provenance of the samples. Although the Grey-headed Albatross and Black-browed Albatross data are directly comparable and largely comprise information from nearly complete squid from fresh samples, those for the two other species are derived from examination of regurgitated beaks, which in the case of Wandering Albatross must derive mainly from squid fed to the chick during the austral winter. Thus we do not know what squid this albatross feeds on when the other three are breeding (and vice versa). Nevertheless, even with these qualifications, the pattern of segregation of squid prey by species and size amongst three types of albatrosses seems a convincing one. White-chinned Petrels, not surprisingly, take mainly much smaller prey amongst which histioteuthids predominate and one or two larger genera like *Taonius* and *Gonatus* occur. They too would seem to be reasonably distinct from the other species in their squid prey.

Elsewhere giant petrels have been recorded to regurgitate squid (Conroy, 1972; Johnstone, 1977) and it was surprising that none were found in the small number of samples collected at Bird Island in 1978–79 (although a few beaks had been found in previous seasons). At Macquarie Island Johnstone (1977) reports *Kondakovia longimana, Taonius, Gonatus* and *Histioteuthis ? eltaninae,* a combination that is reminiscent of Wandering Albatross squid diet, as well as *Nototodarus sloani* Gray, a species apparently particularly common in Australasian waters, and various less certainly identified taxa.

Crustacea

In contrast to squid, where the variety of species available may make it easier to achieve a degree of dietary segregation, the principal crustacean taken by nearly all birds is krill *Euphausia superba* Dana. Only in three species (Dove Prion and the two diving petrels) does it represent much less than 90% of crustacean biomass. For these three species copepods are the other main prey; they predominate by numbers in the diet of Dove Prion and even by weight in that of Common Diving Petrel, the latter thus contrasting quite strongly with the situation in South Georgia Diving Petrel where copepods are much less, and euphausiids much more, important.

Amphipods are ubiquitous, but probably often derive from the stomach contents of larger prey items; only in the smaller petrels are they probably a regular feature of the diet. Large decapods (chiefly *Acanthephyra* spp.) are taken mainly by albatrosses and larger petrels and appear to make a significant contribution to the diet of Light-mantled Sooty Albatross.

In squid the size of prey varied between predators but, in spite of the many bird species of different dimensions to which krill is important, most take mature krill of mean length *c.* 53–55 mm. Blue Petrel and Dove Prion both took smaller Krill (mean length 45 and 41 mm respectively; (Prince, 1980a) and Macaroni Penguin took large numbers (but only 18% by weight) of small, probably 1st year krill of mean length *c.* 20 mm (Croxall & Prince, 1980). The broad picture, however, is clearly one of mature krill being of basic importance to the diet of all species (including Snow Petrel and Cape Pigeon which are not in Table 3) except

King Penguin, Wandering Albatross, Grey-headed Albatross and perhaps Common Diving Petrel.

Nevertheless the minor components of the diet should not always be dismissed as totally insignificant. Careful analysis of the amphipods in the diet of Blue Petrel and Dove Prion showed that there were significant differences in the proportions taken of nearly all of the six species common to the diet of both birds (Prince, 1980a). This also provided some additional evidence for suggestions that some of the dietary differences might be due to prey selection (resulting from different feeding techniques) rather than changes in prey availability.

Carrion

Several seabirds are well known ship-followers, notably giant petrels, Wandering and Black-browed Albatrosses, Cape Pigeons and Wilson's Storm Petrels and the last two and Snow Petrel were common scavengers at whaling stations. It is doubtful nowadays if any of these species subsist to any significant extent upon items scavenged around ships.

Wandering Albatrosses may obtain some of their squid from material regurgitated by Sperm Whales *Physeter catodon* L. (see feeding ecology) and giant petrels certainly derive substantial food from around seal beaches and penguin colonies.

At South Georgia, and Bird Island in particular, the recent population explosion of Antarctic Fur Seal *Arctocephalus gazella* Peters (Payne, 1977) has had some interesting effects on the giant petrel population. Between 1973/74 and 1978/79 the *M. halli* population has increased from fewer than 500 pairs to 1100 pairs, while *M. giganteus* has increased little, if at all (S. Hunter, 1979). This has coincided with the Bird Island fur seal beaches reaching maximum density and with a correlated substantial availability of placentae and pup carcasses in December–January. The difference in the timing of the breeding seasons of these two giant petrels means that such food is available during the chick rearing period only to *M. halli* and may be significantly implicated in the numerical increase of this species. The greater dependence of *M. halli* on beach carrion may also account for indications that *M. giganteus* feeds more at sea and takes a greater proportion of free-living food.

FEEDING ECOLOGY

With the small number of basic prey types available it is not surprising that the distinctions indicated in the previous section between the diet of most species relate to differences in the proportions of these main prey classes taken rather than to absolute prey-specific differences. There are several ways in which information on feeding ecology can contribute to further the picture of resource division and ecological segregation during the breeding season.

First, it may be possible to distinguish differences in species' feeding location, whether in terms of depth or area. Second, the use of particular feeding techniques may reinforce the dietary segregation by being closely correlated with predation of particular organisms. The main feeding methods of the seabirds involved are shown in Table 5.

Table 5. Feeding methods of South Georgia seabirds

Species	Methods						
	Pursuit dive	Plunge	Dive	Surface seize	Dip	Filter	Scavenge
King Penguin	xxx						
Chinstrap Penguin	xxx						
Gentoo Penguin	xxx						
Macaroni Penguin	xxx						
Wandering Albatross				xxx			xx
Black-browed Albatross		x	x	xxx			xx
Grey-headed Albatross		x	x	xxx			x
Light mantled Sooty Albatross		x	?	xxx			x
Southern Giant Petrel				xxx			xxx
Northern Giant Petrel				xxx			xxx
Cape Pigeon				xxx			xx
Snow Petrel				xxx			x
Dove Prion				xx		xxx	
Blue Petrel			xx	xx	xx		
White-chinned Petrel			xxx	xxx			
Common Diving Petrel	xxx	xx	xx	xx			
South Georgia Diving Petrel	xxx	xx	xx	xx			
Wilson's Storm Petrel		x			xxx		x
Black-bellied Storm Petrel		xx			xxx		x
Grey-backed Storm Petrel		xx			xxx		
Blue-eyed Shag	xxx						
Brown Skua							xxx
Southern Black-backed Gull				xxx			xx
Antarctic Tern		xxx			xxx		

xxx: common, xx: occasional, x: rare

Feeding methods

The major division here is between the pursuit-diving species, whether wing-propelled like penguins and diving petrels or foot-propelled like Blue-eyed Shag, and the remainder which are essentially restricted to feeding at the surface of the water.

The penguins are clearly pre-eminently adapted for life as aquatic pursuit-divers. This ability to exploit the water column to a considerable depth must be a substantial advantage over surface restricted species, amply compensating for any reduction in horizontal foraging area consequent on their inability to fly. There are few data on diving depths e.g. Gentoo Penguin caught at 100 m in a trammel net; (Conroy & Twelves, 1972) but it seems likely that the smaller species can easily feed at 100 m. This would be consistent with the depth distribution of large krill concentrations (mainly above 150 m even during the day) and of the fish species taken by Gentoo Penguin (see p. 111). Recent experiments suggest that King Penguins may be able to reach 215 m (G. L. Kooyman, pers. comm.) which compares favourably with a maximum of 265 m recorded for Emperor Penguin (Kooyman, Drabek, Elsner & Campbell, 1971). Blue-eyed Shag has been caught in nets at 25 m (Conroy & Twelves, 1972) and although diving times of up to 2.5 min have been recorded (Kooyman, 1975), comparable with some of those for the smaller penguins (see Conroy & Twelves, 1972; Kooyman, 1975), it is doubtful if they have the same capacity for prolonged diving. The diving petrels are also specialized for diving and swimming underwater, chiefly by reduction in wing

Table 6. Feeding frequency, flight speed and potential foraging range of South Georgia seabirds

Species	Feeding frequency* (days)	Flight speed† (V_{mp}: m s^{-1})	Foraging range‡ (km)
Southern Giant Petrel	< 1	12.5	*c.* 350
Northern Giant Petrel	< 1	12.5	*c.* 350
Gentoo Penguin	1	1.9	31.5
South Georgia Diving Petrel	1 +	7.6	330
Common Diving Petrel	1–1½	8.4	360
Wilson's Storm Petrel	? 1–2	5.7	250
Dove Prion	1–2	6.9	300
Macaroni Penguin	2	1.9	115
Black-browed Albatross	2	10.7	925
Grey-headed Albatross	2	11.0	950
Blue Petrel	2–3	7.0	600
Light-mantled Sooty Albatross	3	9.7	1250
White-chinned Petrel	4	9.5	1650
Wandering Albatross	5–6	12.2	2650
King Penguin	? 5–6	1.9	*c.* 500

* Feeding frequency is interval between successive feeds to chick by same parent.
† Flight and swimming speeds calculated as described in text.
‡ Foraging range calculated on basis of higher feeding frequency.

length so that a 'paddle-like' condition for underwater propulsion is attained (Kuroda, 1967). This has decidedly impaired their flying ability and the species have very high flight speeds (Table 6) and wing loadings, a low buoyancy index (Appendix 2) and a relationship between wing areas and body mass very different from other procellariforms but similar to that of auks Alcidae which they so closely resemble (Warham, 1977: fig. 1). They are certainly not deep divers and may penetrate only a few metres below the sea surface. White-chinned Petrel is probably the only other species that regularly feeds below the surface and then only on very shallow surface dives.

In essence then only penguins, diving petrels and a shag depend on sub-surface foraging techniques. In contrast nearly all albatrosses and petrels take prey at the surface but there are so few field observations that it is not possible to say if there are any variations in the techniques used by different species. There are, however, a few species which mainly detect prey while in flight and either execute a shallow plunge to catch it (Antarctic Tern) or stoop to secure it while still in flight. In the latter category come the very different feeding methods of Wilson's Storm Petrel (pattering over the wave tops) and Blue Petrel (stooping from some height in a manner more typical of the gadfly petrels *Pterodroma* spp.).

Ainley (1977) has indicated that feeding methods may broadly relate to buoyancy indices (see Appendix 2). In Antarctic seabirds there is a much smaller range of such values (2.5–4.0) compared with temperate and tropical species (2.0–5.5). The low values for diving petrels are an integral part of the adaptations for diving and the high ones for storm petrels accord well with the association of such values with the 'dipping' method of feeding (see Ainley, 1977: table 1). Rather surprisingly Blue Petrel has a relatively low buoyancy value but its very low wing loading may be a compensation.

Giant petrels and albatrosses show uniformly low values, except for Light-mantled Sooty Albatross which is recognized as the most aerially adapted of

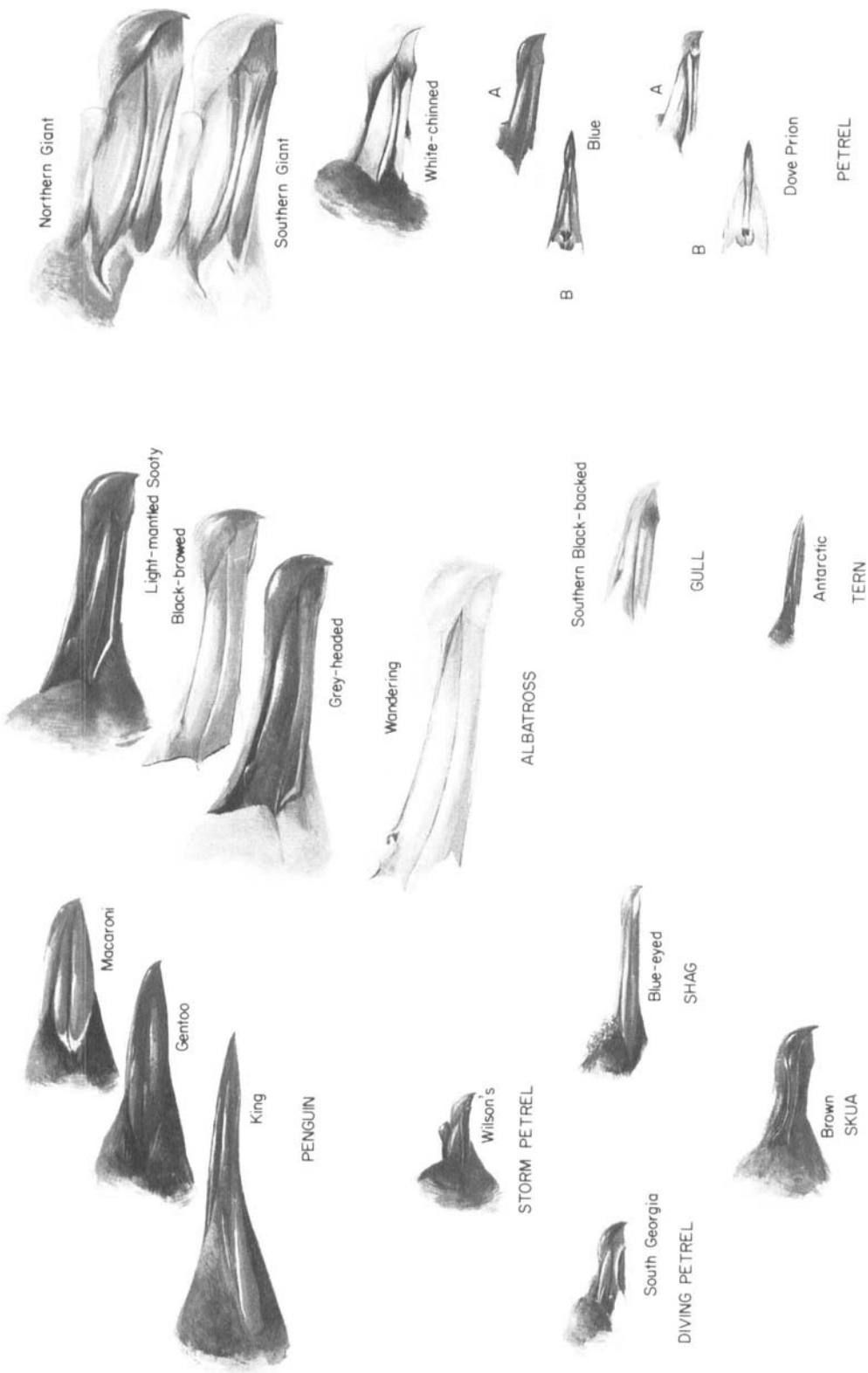

Figure 2. Bills of South Georgia seabirds. King Penguin (x 0.24); Gentoo Penguin (x 0.6); Macaroni Penguin (x 0.24); Wandering Albatross (x 0.5); Grey-headed Albatross (x 0.3); Black-browed Albatross (x 0.3); Light-mantled Sooty Albatross (x 0.3); Southern Giant Petrel (x 0.42); Northern Giant Petrel (x 0.42); White-chinned Petrel (x 0.42); Blue Petrel (x 0.6), A lateral view, B dorsal view; Dove Prion (x 0.6), A lateral view, B dorsal view; Wilson's Storm Petrel (x 0.9); South Georgia Diving Petrel (x 0.9); Blue-eyed Shag (x 0.36); Brown Skua (x 0.3); Southern Black-backed Gull (x 0.36); Antarctic Tern (x 0.48).

albatrosses, although it is unknown what relationship, if any, this has to its feeding methods. It may be noteworthy that the two small fulmarine petrels, Cape Pigeon and Snow Petrel, have rather different indices.

Finally the distinctive feeding technique of Dove Prion is particularly notable whereby, whether hydroplaning (wings outstretched, head just below the surface, propulsion from the feet) or swimming, small prey organisms are filtered by expelling the volume of water taken into the broad, deep bill (see Appendix 2, Fig. 2) through the lamellae fringing the inside of the upper mandible (see Prince, 1980a: plate I). It is this technique that makes it possible to capture vast quantities of small organisms—for example the 41,000 copepods in a food sample weighing only 16 g (Prince, 1980a). The employment of a specialized feeding apparatus thus permits Dove Prion to take substantial quantities of a vastly abundant prey that is clearly quite uneconomic for the other petrels, with bills adapted for picking and seizing, to exploit. In turn a feeding strategy like dipping is probably associated with the capture of larger prey, i.e. those which can be seen while the seabird is in flight. For nearly all prey items Blue Petrel was indeed shown to take larger (and usually significantly so) individuals than Dove Prion (Prince, 1980a). There is also a striking difference in wing loading between Blue Petrel and Dove Prion (see Appendix 2) which is not offset by differences in estimated flight speed (Table 6) and suggests that Blue Petrel uses less energy per unit distance which would fit with its greater dependence on aerial feeding techniques.

Giant petrels, which feed extensively on carrion, seem well adapted for this with relatively short, deep and presumably very powerful bills for tearing flesh from carcasses and it is possible that the flattened occiput of their skull represents an adaptation for inserting the head into carcasses.

The species that mainly use surface seizing techniques show a wide variation in bill size and shape (see Appendix 2, Fig. 2). Ashmole (1968) discussed extensively the relationships between bill size and shape and prey size in five species of sympatric tropical terns. Four of these species had bills of very similar lengths but differed more in depth (and hence cross-section area) and there was some correlation between bill stoutness and prey size although this was complicated by the influence of body size whereby smaller birds (with bill not always in proportion) tended to take very much smaller prey.

Here, although there are probably some relationships between bill shape and prey type (e.g. Gentoo with its more dagger-shaped bill being the small penguin which takes significant fish in its diet), there is little indication of correlation between bill size and crustacean prey size, although large decapods (especially *Acanthephyra*) seem principally to be taken by the larger petrels and albatrosses and copepods by the smaller petrels. There is insufficient information on fish dimensions to do other than confirm that petrels take much smaller prey than penguins and albatrosses. The differences in the dimensions of squid taken by albatrosses have already been noted, with Wandering Albatrosses taking many squid of mean weight 3 kg, Grey-headed and Black-browed Albatrosses squid of *c.* 200 g (although some individuals of up to 1200 g were found) and Light-mantled Sooty Albatross a combination of squid weighing 80 g and *c.* 700 g. It is not clear why the latter, which is the smallest albatross, regularly takes squid substantially larger than those taken by the slightly larger mollymauks. Equally it has been noted elsewhere (Clarke *et al.*, in press) that 3 kg *Kondakovia* are

themselves active, very well-armed predators and an albatross must be very adept to take such squid alive. It is certain that Wandering Albatrosses do scavenge the remains of some squid (e.g. of 6 kg + *Taningia*) probably from sperm whale vomit and it might be suggested that *Kondakovia* (and the *Discoteuthis* in Light-mantled Sooty Albatross diet) are taken in a similar manner. Evidence for and against this has been presented by Clarke *et al.* (in press) and we believe that, on balance, the long, powerful, razor-sharp and hook-tipped bills of these albatrosses are sufficiently effective to immobilize even quite large squid once they are impaled.

This in turn raises the question of how such active species as squid and fish can be approached by birds feeding at the surface and, apart from occasional records of surface plunging by mollymauks, there are no direct observations. It seems likely to us that squid and fish are often associated, as predators, with krill swarms and that as these rise to the surface (vertical migration) at night the predators accompany them and become available to petrels and albatrosses sitting, essentially invisible from below, on the surface.

The topic of nocturnal feeding by seabirds on vertically migrating marine organisms was reviewed by Imber (1973) who also drew attention to the high numbers of bioluminescent squid and fish (especially myctophids) taken by certain sea-birds and suggested that these prey were detected by their nocturnal light emissions. As more squid are bioluminescent than not and most have downwardly directed photophores, bioluminescent species may not, in fact, be especially vulnerable. Concentrations of bioluminescent krill may, however, be particularly visible and attractive to night-feeding seabirds—both krill-feeding species and those that gather in anticipation of catching the associated predators.

Although all seabirds will presumably take suitable prey at whatever time of day it is available, diurnal feeding on live prey has been recorded for few species. To judge either from times of chick feeding or actual observations it may be of some importance to Cape Pigeon, Snow Petrel, giant petrels (which are unusual in feeding chicks both by day and night (S. Hunter, 1979)), Dove Prion and Wilson's Storm Petrel, although these last two do not feed their chicks until after dusk, presumably to reduce predation by skuas.

Pursuit-diving species would be expected to be much less restricted to nocturnal feeding than the surface feeders. It is not surprising, therefore, that all penguins regularly spend the night ashore in the colony on the conclusion of a feeding trip and proportionately must spend much more time feeding diurnally than nocturnally, especially while raising chicks. Thus a fundamental difference in feeding ecology (diving versus surface feeding) may also be associated, to some extent, with different temporal patterns of predation.

Foraging range

Species with similar breeding seasons, diets and foraging methods may still be adequately separated ecologically, if there is sufficient difference in their feeding zones. Examples of this have been provided by Ashmole & Ashmole (1967) for two tropical terns *Anous stolidus* (L.) and *Sterna fuscata* L. and Cody (1973) for a number of northern hemisphere auks. In both these cases much of the evidence rested on field observations of feeding birds but, as noted earlier, there are few such observations of Antarctic seabirds and especially so for birds of known breeding status and provenance.

In the absence of such information the interval between successive feeds brought to a chick by one parent can be used as an index of the distance travelled to find food. In Table 6 the species are arranged in order of increased duration of foraging trips (and therefore decreased frequency of feeding chicks).

In this paper we have chosen to use rather broad time categories for feeding frequency. For a number of the species we have much more precise data on the frequency with which a chick is fed, either derived from direct observations or the use of electronic recording devices in burrows to record the visits of parents, or from series' of chick weighings at 3 h intervals to detect feeds more accurately. Unfortunately we do not yet have such information for all the species concerned, nor are data from each source fully compatible. Pending a more thorough evaluation of all features of relevant data we have used simplified categories here, which may well mask some interspecific differences.

The species range from those where each parent feeds the chick daily (Gentoo Penguin usually has two chicks; all other species have only one) to those in which each parent may be absent for nearly a week. If there is any discontinuity in the distribution of species by foraging range it probably lies between species in which both parents feed chicks daily (e.g. giant petrels, diving petrels, often Dove Prion and probably Wilson's Storm Petrel) and those where each parent tends to feed the chick no oftener than on alternate days. This might represent a distinction between inshore and offshore feeding species and what few field observations exist would tend to confirm this. Thus all species in the first group are not infrequently seen feeding by land-based observers; none of the other species have ever been so observed at South Georgia.

In the absence of additional information it is impossible to make further subdivision (e.g. into a coastal-inshore-offshore-pelagic sequence) that might relate to the location of certain hydrographic features, e.g. continental shelf (*c.* 75 km wide), Antarctic Convergence *c.* 300 km distant. It is clear that some species (e.g. Wandering Albatross, White-chinned Petrel, Light-mantled Sooty Albatross) have the capacity for highly pelagic foraging and this is certainly supported by the presence of a number of squid in the diet of Wandering Albatross associated with warmer waters to the north of the Antarctic Convergence (Clarke *et al.*, in press).

It is possible to gain a rough idea of potential foraging ranges of these species by considering the length of absence on a feeding trip together with flight (or swimming for penguins) speed. Using the method of Pennycuick (1969), values for minimum power speed, *Vmp* (essentially speed at which fuel is used most slowly and probably near the lower limits of a bird's flight speed range) have been derived using body weight data from Appendix 2 and wing span values mainly from Warham (1977) supplemented by unpublished data for Blue Petrel and South Georgia Diving Petrel. Kooyman (1975) suggested that penguins usually swim at 7–10 km h^{-1} and the lower value has been used to obtain the range estimates given here.

It should be stressed that these estimates are probably far from accurate, perhaps especially for the inshore species, as they assume a straight, direct flight path and no stops for feeding. In spite of these deficiencies it is instructive to examine the findings for taxonomically and ecologically related species.

Feeding range information has not shown up any obvious distinctions between the two *Diomedea* mollymauks, the two giant petrels (although there is

circumstantial evidence that *M. giganteus* spends more time at sea than *M. halli*) or the two diving petrels (although Payne & Prince (1979) from a detailed analysis of chick weight changes, noted that *P. georgicus* chicks are fed more assiduously than those of *P. u. exsul*). The largest and smallest albatrosses would appear to be more pelagic than the others.

The potential for Blue Petrel to feed further from the breeding site is indicated and this is supported (Prince, 1980a) by more detailed evidence from chick weighings, the occurrence of South Shetland Island derived pumice in the stomachs of 40% of Blue Petrels but only 2% of Dove Prions and the occurrence of twice as much oil (product of digestion of solid food) in Blue Petrel samples.

The difference between the two penguins is even more striking with average feeding trips of Gentoo usually lasting *c.* 9 h and those of Macaroni *c.* 33 h. This inshore: offshore distinction is supported by the fish taken by Gentoo (see p. 111) belonging to the size classes of species which are known to frequent inshore kelp beds during maturation and by the much greater degree of digestion of krill of the same size in Macaroni samples than in Gentoo (Croxall & Prince, 1980). It is also plausible that Gentoo, seeking to raise two chicks, should be more restricted in its foraging range than Macaroni with only a single offspring.

A little additional information can be deduced from general observations of birds at sea during the breeding season. The overall distribution of records indicates that Light-mantled Sooty Albatrosses, in contrast to the other albatrosses, are rarely seen to the north of South Georgia and that Blue Petrel also has a distinct southerly bias to its records. This may provide some indication of a directional bias in foraging activity that could not be deduced from information on mean foraging distance and it is interesting that the two most pelagic albatrosses should differ quite markedly in this respect.

We do not, of course, have any direct evidence of the use of different feeding areas or zones by those species with similar dietary requirements and breeding seasons and the possibility that the 'offshore' species merely collects food more slowly over the same general area as the 'inshore' one can only be regarded as inherently unlikely (and unsupported by the appropriate visual observations).

On the other hand Macaroni penguins certainly catch some krill close to land on their return trips as the top few krill in the stomach are usually hardly digested. Nevertheless they must be subject to less direct competition once out of the range of Gentoo Penguins and in terms of swimming efficiency it would make sense to do this journey with as little extra body weight as possible.

We have already noted that there are numerous warmer-water squid in the diet of Wandering Albatross, indicative of lengthier trips to the north of South Georgia, than in the food of the other *Diomedea* spp. With better knowledge of the local distribution of marine stocks we might be able to interpret the occurrence of small *E. superba* only in Macaroni samples or lampreys only in Grey-headed Albatross samples in terms of feeding areas.

DISCUSSION

In this paper we have tried to describe the biology and adaptations of South Georgia seabirds in relation to their ecological segregation in the breeding season and in particular to the way in which the resources of the marine environment are partitioned.

It seems clear that temporal, dietary and geographical distinctions are each important and, indeed, it seems unlikely that any one mechanism by itself is adequate to achieve a sufficient degree of reduction in direct competition, if all species in the seabird community are considered together. Thus although Wandering Albatross breeds in winter it is likely that it takes different squid from other albatrosses even at other times of year. The diving petrels and the Blue Petrel-Dove Prion species pair have non-overlapping periods of chick rearing but, in addition, they have some clear differences in diet and associated adaptations. The two smaller penguins differ partly in diet and partly in feeding range. In citing these examples we are looking at the most similar pairs of species and only for the giant petrels (which are presently being studied) can we not yet see well-marked ecological differences.

We would re-emphasize, however, that the species of the community employ all of the main mechanisms in different combinations and proportions and that as a whole the community makes up a complex, dynamic pattern of interacting adaptations many facets of which still remain to be understood. In Table 8 we have set out in simplified diagrammatic form what we consider to be the way in which the more important ecological isolating mechanisms operate.

Unlike tropical seabirds where substantial diversity in the timing of breeding seasons is shown (Harris, 1969; Schreiber & Ashmole, 1970), in high latitudes there is little room for manoeuvre. At South Georgia winter breeding is an unusual strategy with Wandering Albatross its chief exponent, as the time of principal demand for food by King Penguin populations is almost certainly in summer. At this time, however, it is the only real subsurface avian squid predator but it may well be in substantial competition earlier in the season with Southern Elephant Seal *Mirounga leonina* L. which also eats squid and fish. The feeding activity of the large South Georgia population of this seal (170,000 tonnes biomass by 1960 (Laws, 1960) and certainly over 200,000 tonnes nowadays) before and during its August–October breeding season may compel King Penguin to delay the onset of breeding.

The distinction between diving and surface feeding is clearly a fundamental one and it is doubtful if there is much competition between members of the two categories, particularly as there are likely to be differences in the time of day when much of the predation occurs.

The subsurface feeders appear segregated chiefly by diving capacity and diet but it would be interesting to know to what extent the large fur seal population (369,000 seals with a biomass of 14,500 tonnes (Payne, 1979) at South Georgia (and particularly Bird Island), compete with the small penguins. This fur seal seldom dives below 68 m (G. L. Kooyman, pers. comm.) and its prey is principally krill, some fish and a little squid.

For Gentoo and Macaroni Penguins, and a number of surface-feeding seabirds, differences in foraging range seem significant. The distinction between inshore and offshore feeding seabirds is often regarded as an important one and correlated with certain other biological adaptations of the species concerned. Thus Lack (1968) suggested that in many families of marine birds offshore feeders breed in larger more widely spaced colonies, have smaller clutches, longer incubation and fledging periods, longer incubation shifts, reduced chick feeding frequency but higher chick peak weights relative to adult weights and later sexual maturity compared with inshore feeders and that the differences are

principally related to food availability. Cody (1973) added slower growth rates, and feed size a smaller proportion of adult body weight from his studies of northern hemisphere auks where he regarded differences in feeding zones as the principal ecological isolating mechanism.

In addition, on the basis of data for two storm petrels *Oceanodroma,* Ainley *et al.* (1975) suggested that the lower wing loadings of offshore feeders may be adaptive in reducing the energy used per unit distance flown. The wing loadings of Dove Prion and Blue Petrel (Appendix 2) are in line with this but Warham (1977) has noted that lower wing loading is usually correlated with slower flight speed which may be a countervailing disadvantage and the whole topic clearly needs critical re-investigation.

Finally it is worth noting that the poorly synchronized breeding species (Gentoo Penguin, storm petrels, see p. 106) all seem to be inshore feeders and perhaps worth speculating whether this asynchrony in breeding timetable may be an adaptive mechanism for reducing intraspecific competition in the restricted inshore waters by spreading the peak demand for food more evenly over a longer period.

It is of interest briefly to see to what extent the information presented here corroborate the general picture developed by Lack (1968). Some additional relevant data are given in Table 7, with the species still placed in order of feeding frequency. Although some of the meal size data are very approximate (and derived variously from interpretation of food sample and chick growth increment data) there is no indication of any fixed relationship between it and body weight (cf. Cody, 1973) and only the diving petrel values (derived from chick growth increment analysis) stand out as anomalous and it remains to be seen if this persists when other species' diets are analysed similarly.

Likewise there is no clear relationship between feeding zone and growth rate. However, if Cody's (1973) data are reanalysed relative to the size of the bird (rather than just as absolute weight increases), as his smaller species (with smallest absolute growth but high *relative* growth) were feeding farthest from land there is no correlation for his species either. Equally, nothing clear cut can be derived from the data on the amount by which chicks at peak weight exceed adult weight, a statistic reflecting the extent of fat reserves and hence the degree to which the chicks are insured against variations in feeding frequency, likely to be greatest in offshore foraging birds.

At the level of the 'species-pair', however, one is able to see some of the logic behind the earlier generalizations. Thus, in contrast to the inshore feeding Gentoo Penguin, the offshore feeding Macaroni Penguin breeds in few, vast colonies (no need to reduce the intraspecific competition that would be generated by excessive clumping of inshore feeders) has only one not two chicks, has month-long incubation periods not daily changeovers, makes fewer, longer feeding trips (though the single chick gets fed daily just as do those of Gentoo) and probably does not breed until at least six years of age (Carrick, (1972) on another subspecies, Royal Penguin *E. chrysolophus schlegeli* Finsch) whereas if Gentoo is similar to its congeners it may commence breeding at three years of age (Le Resche & Sladen, 1970; Ainley, 1975; Ainley & De Master, in press). On the other hand incubation periods are similar and Macaroni chicks have faster growth and much shorter fledging periods. Many of these adaptations probably relate to the different requirements imposed by trying to raise two chicks rather

Table 7. Meal sizes and chick growth statistics for South Georgia seabirds

Species	Meal size		Chick growth*			Reference
	Mean (g)	As % adult weight	Mean wt gain ($g.d^{-1}$)	As % peak weight	Peak wt as % adult wt	
Southern Giant Petrel	*c.* 500	10	79	1.3	116	S. Hunter, 1979
Northern Giant Petrel	*c.* 500	10	66	1.2	108	S. Hunter, 1979
Gentoo Penguin	860	15	85	1.7	91	Croxall, unpublished data
South Georgia Diving Petrel	*c.* 40	30	4.8	3.3	136	Payne & Prince, 1979
Common Diving Petrel	*c.*40	37	4.0	2.6	120	Payne & Prince, 1979
Wilson's Storm Petrel	*c.* 5	13	1.3/2.5	2.0/3.6	158/182	Beck, 1972/Lacan, 1971
Dove Prion	*c.* 25	15	6.5	3.1	128	Prince, unpublished data
Macaroni Penguin	690	15	70	2.2	67	Croxall, unpublished data
Black-browed Albatross	570	15	70	1.4	132	Prince, unpublished data
Grey-headed Albatross	600	16	63	1.3	124	Prince, unpublished data
Blue Petrel	*c.* 35	18	7	2.4	150	Prince, unpublished data
Light-mantled Sooty Albatross	510	18	45	1.3	121	Thomas, unpublished data
White-chinned Petrel	*c.* 150	11	24	1.3	135	Prince, unpublished data
Wandering Albatross	750	9	56	0.5	132	Tickell, 1968
King Penguin	*c.* 2000	13	*c.*120	1.1	80	Stonehouse, 1960

* Growth calculated over period $t_{10} - t_{90}$: see Ricklefs (1973)

than one and can perhaps be seen as ecologically alternative strategies. It is not clear, however, what the significance is of the extremely long incubation and brooding shifts in Macaroni Penguin.

The later sexual maturity in Macaroni Penguin might be explained by postulating greater intraspecific competition for food amongst the breeding (and potentially breeding) population thus favouring a delay in first breeding attempts. A rough indication that this might be so is obtained by calculating the volume of ocean available to each individual of the breeding population of each species at South Georgia (see Table 1) within the estimated foraging range (Table 6) and for a feeding depth of 100 m, assuming a circular feeding area around a point source. For Gentoo the result is 1558×10^3 m^3 per bird whereas for Macaroni it is only 419×10^3 m^3 per bird. Thus although the Macaroni Penguin population has over 13 times the sea volume at its disposal their 50 times greater abundance more than offsets this advantage.

Comparing the inshore Dove Prion with the more offshore Blue Petrel is somewhat less convincing as, against predictions, the latter is less abundant, has shorter incubation and fledging periods (but does show longer incubation shifts) and less frequent chick feeding (but larger feeds). With the two mollymauks meal size, feeding frequency, incubation shifts and incubation periods and abundance are similar (at South Georgia: Black-browed Albatross is much more abundant on a world population basis), and only the duration of the fledging and pre-laying attendance periods are different. Nevertheless Black-browed Albatross breeds at an earlier age and annually thereafter whereas Grey-headed Albatross breeds later and biennially when successful in raising a chick.

Thus in examining more closely three species-pairs we find, compared with predictions, reasonably good fits (penguins), poor fits (petrels) and species where major biological differences are barely indicated by differences in the range of adaptations surveyed. This is not to challenge the theoretical basis on which the generalizations rest nor their heuristic value nor the fact that all of them are supported by some species in some situations. It is rather to emphasize that with some Antarctic species we may have reached the stage where it will be possible, and preferable, on the basis of improved knowledge of appropriate details of the species' biology, to understand some of the key interrelationships between adaptations and ecological strategies, rather than to generate modified generalizations.

There is, both throughout the paper and in Table 8, a considerable emphasis on the importance of diet and its associated adaptations. This is partly because feeding studies form much of our work at South Georgia and partly because we believe that insufficient detailed quantitative attention has been given to this topic. For instance we wonder whether, if Cody had had available comprehensive dietary information (of the kind produced by Bedard (1969b) for three Alaskan auklets), he would have still maintained the over-riding importance of feeding zone separation.

We recognize that our own dietary data derive, in most cases, only from a single season's work and it may therefore be premature to regard them as fully typical. Nevertheless we would affirm the view, implicit in many of Lack's (1968) seabird analyses, that a knowledge of feeding ecology may be the key to understanding many other adaptations; in particular we believe that detailed knowledge of dietary composition by weight and nutritive value, of meal size and

Table 8. Principal mechanisms for ecological segregation in the breeding season for South Georgia seabirds

Winter		Summer
Diving		*Diving*
King Penguin	Inshore	
	Fish:	Blue-eyed Shag
		Gentoo Penguin
	Krill:	Gentoo Penguin
	Offshore	
	Krill:	Macaroni Penguin
	Squid:	King Penguin
Surface Feeding		*Surface Feeding*
Wandering Albatross	Squid:	White-chinned Petrel
		Light-mantled Sooty Albatross
		Grey-headed Albatross
	Copepods:	Common Diving Petrel
		Dove Prion
	Krill	
	Inshore:	Common Diving Petrel (early)
		South Georgia Diving Petrel (late)
		Wilson's Storm Petrel
		Dove Prion
	Offshore:	Blue Petrel
		Black-browed Albatross
	Carrion:	Giant Petrels

feeding frequency in relation to chick growth rates are fundamental elements within this.

In saying this we imply that there may be important relationships between the above factors and it is appropriate here briefly to mention how they relate to the main differences between the two mollymauks (see p. 125). Prince (in prep.) has shown, particularly by following the growth of chicks raised from eggs by parents of the opposite species, that the difference in fledging times between these two species is principally due to differences in the composition of the diet fed to the chicks (the squid that predominates in Grey-headed Albatross diet being a much less nutritive resource than the krill which forms the bulk of Black-browed Albatross diet). It is likely also that the predominantly squid diet is implicated in the inability of successful Grey-headed Albatrosses to regain breeding condition in time to lay the following season. Thus, differences in dietary composition may be involved in fundamental differences in breeding strategy.

It has been implicit throughout this paper that most of the identified differences between species are the result of competition in the past and subsequent attempts by the birds to minimize the continuing effects of this. Some authors (e.g. Salomonsen, 1955; Beck, 1970) have contended that the abundance of suitable food is such that seabirds do not compete but most workers have been more impressed by the consequences of seasons of food shortage (Belopolskii, 1957; Ashmole, 1963, 1971; Croxall & Prince, 1979) and have concluded that it is often the availability of appropriate prey rather than its actual existence or abundance that is the critical factor.

As with most similar analyses direct evidence of interspecific competition is lacking and much of the circumstantial evidence (the exact nature of the ecological differences, evidence for the selection of certain prey items when

others are available and being taken by other species) has elements of circularity in its reasoning.

In 1977-78, however, commercial fishing operations around South Georgia were unable to locate krill in swarms and there was an unprecedented failure of krill-eating seabirds, especially Gentoo Penguin and Black-browed Albatross, to raise their chicks (Croxall & Prince, 1979). In contrast Grey-headed Albatrosses, feeding mainly on squid (which themselves may have been feeding extensively on the astonishingly abundant amphipod *Parathemisto gaudichaudii* Guérin Meneville) had their best breeding season. It would appear significant that Black-browed Albatrosses, which do take squid,were unable sufficiently to switch to this resource to improve their breeding success and not implausible that direct competition with predominantly squid-eating Grey-headed Albatrosses may have been responsible.

This analysis has been exclusively concerned with the ecological picture during the breeding season. The lack of data on diet in winter makes it difficult to comment on the basis of segregation at that season. All species undoubtedly range much more widely once breeding is concluded. Diversity in the area is reduced as several species depart, notably Wilson's Storm Petrel, a migrant to the northern hemisphere, and Black-browed Albatross, moving north to warmer waters, chiefly off South Africa (Tickell, 1967). Some species, e.g. giant petrels, diving petrels, Gentoo Penguins, as well as Cape Pigeon and Snow Petrel, are seen at South Georgia throughout the winter and others such as Grey-headed Albatross certainly remain in high latitudes. There are thus indications that one member of at least two species-pairs may be considerably more migratory than the other. In the case of the albatrosses and the penguins the species that remains is that least dependent on euphausiid prey, a resource of minimal availability in winter, in contrast to squid and fish which are able to sustain breeding Wandering Albatrosses and King Penguins.

None of this information gives any indication whether competition for food for any of these species is more intense in summer or winter. The heavy demands during chick rearing (and particularly for penguins where a complete moult necessitating the development of enormous fat reserves immediately follows), lead us to think that the summer period may be the most critical.

Finally, why are certain South Georgia seabirds distinctly uncommon as breeding species and why do some other species not occur there? Although Rockhopper and Macaroni Penguins are probably respectively warmer and colder water replacement species they co-exist at Macquarie Island and at Marion Island. It is not clear why Rockhopper is not commoner at South Georgia unless the large population of Gentoo Penguins offers too much competition in inshore areas. The abundance of the two small penguins may also be restricting the expansion of Chinstrap Penguin (see Croxall & Kirkwood, 1979) which takes krill and is probably somewhat intermediate in its foraging range (Croxall & Furse, 1980). It may be significant that Chinstrap is most abundant at the southeast end of the island, where there is a much smaller concentration of Macaroni Penguins.

The small fulmarine petrels (Cape Pigeon and Snow Petrel) and the other storm petrels are all at a limit of their breeding range at South Georgia but it is uncertain why they are not more abundant. Cape Pigeon is a particular puzzle as it is abundant in the area in both summer and winter yet the breeding population is very small.

At more northerly subantarctic islands (e.g. Crozet, Marion) a slightly greater diversity of seabirds than at South Georgia does occur. The additional species can be divided into three categories:

(a) warmer water congeners of the colder water species, e.g. Sooty Albatross *Phoebetria fusca* (Hilsenberg) and various prions *Pachyptila* (some with and some without the filtering lamellae), the prions often with some differences in breeding habitat and timing of the breeding season,
(b) gadfly petrels *Pterodroma* spp., a group typical of warmer water and specializing in in 'dipping' feeding techniques,
(c) winter breeding medium-sized petrels (e.g. Grey Petrel *Procellaria cinerea* Gmelin and Great-winged Petrel *Pterodroma macroptera* (A. Smith)).

All the additional species seem to derive from the greater proximity of these slightly more northerly islands to warmer waters and perhaps from the generally milder climate giving a longer effective breeding season and permitting a greater variety of species to breed in winter.

However it is probable that the marine environment surrounding these islands may not be as rich in food resources as the South Georgia area and it would be of great interest to know how the abundance and ecology of the typically sub-Antarctic species are affected under these circumstances.

ACKNOWLEDGEMENTS

We should like to thank Dr D. G. Ainley, Dr M. R. Clarke, I. Hunter, S. Hunter and G. Thomas for making available their unpublished data, Drs K. R. Kerry and G. L. Kooyman for allowing us to use their personal communications and Drs R. M. Laws and C. M. Perrins for comments on the manuscript. We are most indebted to Bruce Pearson for providing Fig. 2.

REFERENCES

AINLEY, D. G., 1975. Development of reproductive maturity in Adelie Penguins. In B. Stonehouse (Ed.), *The Biology of Penguins:* 139–157. London: Macmillan.

AINLEY, D. G., 1977. Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In G. A. Llano (Ed.), *Adaptations within Antarctic Ecosystems:* 669–685. Washington: Smithsonian Institution.

AINLEY, D. H. & DEMASTER, D. P., in press. Survival and mortality in a population of penguins. *Ecology.*

AINLEY, D. G., MORRELL, S., LEWIS, T. J., 1974. Patterns in the life histories of storm petrels on the Farallon Islands. *Living Bird, 13:* 295–312.

ASHMOLE, N. P., 1963. The regulation of numbers of tropical oceanic birds. *Ibis, 103b:* 458–473.

ASHMOLE, N. P., 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Systematic Zoology, 17:* 292–304.

ASHMOLE, N. P., 1971. Seabird ecology and the marine environment. In D. S. Farner and J. R. King (Eds.) *Avian Biology, Vol. 1:* 112–286. New York: Academic Press.

ASHMOLE, N. P. & ASHMOLE, M. J., 1976. Comparative feeding ecology of sea birds of a tropical oceanic island. *Bulletin of the Peabody Museum of Natural History, 24:* 1–131.

BARRAT, A., 1976. Quelques aspects de la biologie et de l'écologie du Manchot royal (*Aptenodytes patagonica*) de l'île de la Possession, archipel Crozet. *Comite National Français des Récherches Antarctiques,* No. *40:* 9–52.

BECK, J. R., 1969. Food, moult and age of first breeding in the Cape Pigeon, *Daption capensis* Linnaeus. *British Antarctic Survey Bulletin,* No. *21:* 33–44.

BECK, J. R., 1970. Breeding seasons and moult in some smaller Antarctic petrels. In M. W. Holdgate (Ed.), *Antarctic Ecology:* 542–550. London: Academic Press.

BECK, J. R. & BROWN, 1972. The biology of Wilson's Storm Petrel *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. *Scientific Report of the British Antarctic Survey,* No. *69:* 1–54.

BEDARD, J., 1969a. Histoire naturelle du Gode, *Alca torda* L., dans le golfe Saint Laurent, Province de Québec, Canada. *Etude de Service Canadien de la Faune,* No. 7. Ottawa.

BEDARD, J., 1969b. Feeding of the Least, Creasted and Parakeet Auklets around St. Lawrence Island, Alaska. *Canadian Journal of Zoology, 47:* 1025–1050.

BELOPOLSKII, L. O., 1957. *Ecology of Sea Colony Birds of the Barents Sea.* Israel Program of Scientific Translations, 1961.

BURGER, A. E., 1978. Interspecific breeding attempts by *Macronectes giganteus* and *M. halli. Emu, 78:* 234–5.

CARRICK, R., 1972. Population ecology of the Australian Black-backed Magpie, Royal Penguin and Silver Gull. In *Population Ecology of Migratory Birds: A Symposium. U.S. Department of the Interior Wildlife Research Report,* No. 2: 41–99.

CARRICK, R. & INGHAM, S. E., 1967. Antarctic sea-birds as subjects for ecological research. *Proceedings of the Symposium on Pacific-Antarctic Sciences, Tokyo, 1966. JARE Scientific Report, Spec. 1:* 151–184. Tokyo: Department of Polar Research.

CARRICK, R. & INGHAM, S. E., 1970. Ecology and population dynamics of antarctic seabirds. In M. W. Holdgate (Ed.), *Antarctic Ecology:* 505–525. London: Academic Press.

CLARKE, M. R. & PRINCE, P. A., in press. Cephalopod remains in regurgitations of Black-browed and Grey-headed Albatrosses at South Georgia. *British Antarctic Survey Bulletin.*

CLARKE, M. R., CROXALL, J. P. & PRINCE, P. A., in press. Cephalopod remains in regurgitations of the Wandering Albatross at South Georgia. *British Antarctic Survey Bulletin.*

CODY, M. L., 1973. Coexistence, coevolution and convergent evolution in seabird communities. *Ecology, 54:* 31–44.

CONROY, J. W. H., 1972. Ecological aspects of the biology of the giant petrel *Macronectes giganteus* (Gmelin) in the Maritime Antarctic. *Scientific Report of the British Antarctic Survey,* No. 75: 1–74.

CONROY, J. W. H. & TWELVES, E. L., 1972. Diving depths of the Gentoo Penguin (*Pygoscelis papua*) and Blue-eyed Shag (*Phalacrocorax atriceps*) from the South Orkney Islands. *British Antarctic Survey Bulletin,* No. 30: 106–108.

CROXALL, J. P., 1979. Distribution and population changes in the Wandering Albatross *Diomedea exulans* L. at South Georgia. *Ardea, 67:* 15–21.

CROXALL, J. P. & FURSE, J. R., 1980. Food of Chinstrap Penguins *Pygoscelis antarctica* and Macaroni Penguins *Eudyptes chrysolophus* at Elephant Island group, South Shetland Islands. *Ibis, 122:* 237–245.

CROXALL, J. P. & KIRKWOOD, E. D., 1979. *The Breeding Distribution of Penguins on the Antarctic Peninsula and the Islands of the Scotia Sea.* Cambridge: British Antarctic Survey.

CROXALL, J. P. & PRINCE, P. A., 1979. Antarctic seabird and seal monitoring studies. *Polar Record, 19:* 573–595.

CROXALL, J. P. & PRINCE, P. A., 1980. The food of Gentoo Penguins *Pygoscleis papua* and Marcaroni Penguins *Eudyptes chrysolophus* at South Georgia. *Ibis, 122:* 245–253.

FOXTON, P., 1956. The distribution of the standing crop of zooplankton in the Southern Ocean. *'Discovery' Reports, 28:* 191–236.

FOXTON, P., 1964. Seasonal variations in the plankton of Antarctic waters. In R. Carrick, M. W. Holdgate & J. Prevost (Eds.), *Biologie Antarctique:* 311–318. Paris: Hermann.

HARRIS, M. P., 1969. Breeding seasons of seabirds in the Galapagos Islands. *Journal of Zoology, 159:* 145–165.

HART, T. J., 1942. Phytoplankton periodicity in Antarctic surface waters. *'Discovery' Reports, 21:* 261–356.

HUNTER, I., 1979. *Burrow-dwelling petrel survey and census, Bird Island, South Georgia. Progress Report 1978–79.* British Antarctic Survey unpublished manuscript.

HUNTER, S., 1979. *Report on giant petrel fieldwork 1978–79.* British Antarctic Survey unpublished manuscript.

IMBER, M. J., 1973. The food of Grey-faced Petrels *Pterodroma macroptera gouldi* (Hutton), with special reference to diurnal vertical migration of their prey. *Journal of Animal Ecology, 42:* 645–662.

IMBER, M. J., 1976. Comparison of the prey of the black *Procellaria* petrels of New Zealand. *New Zealand Journal of Marine and Freshwater Research, 10:* 119–130.

JOHNSTONE, G. W., 1977. Comparative feeding ecology of the giant petrels *Macronectes giganteus* (Gmelin) & *M. halli* (Mathews). In G. A. Llano (Ed.), *Adaptations within Antarctic Ecosystems:* 647–668. Washington: Smithsonian Institution.

KOOYMAN, G. L., 1975. The physiology of diving in penguins. In B. Stonehouse (Ed.), *The Biology of Penguins:* 115–137. London: Macmillan.

KOOYMAN, G. L., DRABEK, C. M., ELSNER, R. & CAMPBELL, W. B., 1971. Diving behaviour of the Emperor Penguin, *Aptenodytes forsteri. Auk, 88:* 775–795.

KURODA, N. H., 1967. Morpho-anatomical analysis of parallel evolution between diving petrel and ancient auk, with comparative osteological data of other species. *Miscellaneous Reports of the Yamashina Institute of Ornithology and Zoology, 5, 2(28):* 111–137.

LACAN, F., 1971. Observations écologiques sur le pétrel de Wilson (*Oceanites oceanicus*) en Terre Adélie. *Oiseau Revue de Française Ornithologie, 41,* Special number: 65–89.

LACK, D., 1934. Habitat distribution in certain Icelandic birds. *Journal of Animal Ecology, 3:* 81–90.

LACK, D., 1968. *Ecological Adaptations for Breeding in Birds.* London: Methuen.

LAWS, R. M., 1960. The Southern Elephant Seal *Mirounga leonina* on South Georgia. *Norsk Hvalfangsttidende, 49:* 520–542.

LeRESCHE, R. E., & SLADEN, W. J. L., 1970. Establishment of pair and breeding site bonds by young known-age Adelie Penguins *Pygoscelis adeliae. Animal Behaviour, 18:* 517–526.

PAYNE, M. R., 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society (B), 279:* 67–79.

PAYNE, M. R., 1979. Growth in the Antarctic Fur Seal *Arctocephalus gazella*. *Journal of Zoology, 187:* 1–20.

PAYNE, M. R. & PRINCE, P. A., 1979. Identification and breeding biology of the diving petrels *Pelecanoides georgicus* and *P. urinatrix exsul* at South Georgia. *New Zealand Journal of Zoology, 6:* 299–318.

PEARSON, T. H., 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. *Journal of Animal Ecology, 37:* 521–552.

PENNYCUICK, C. J., 1969. The mechanics of bird migration. *Ibis, 111:* 525–556.

POTTER, I. C., PRINCE, P. A. & CROXALL, J. P., 1979. Data on the adult marine and migratory phases in the life cycle of the Southern Hemisphere lamprey, *Geotria australis* Gray. *Environmental Biology of Fishes, 4:* 65–69.

PRINCE, P. A., 1980a. The food and feeding ecology of Blue Petrel (*Halobaena caerulea*) and Dove Prion (*Pachyptila desolata*). *Journal of Zoology, 190:* 59–76.

PRINCE, P. A., 1980b. The food and feeding ecology of Grey-headed Albatross *Diomedea chrysostoma* and Black-browed Albatross *D. melanophris*. *Ibis, 122.*

PRINCE, P. A. & PAYNE, M. R., 1979. Current status of birds at South Georgia. *British Antarctic Survey Bulletin,* No. *48:* 103–118.

RICHDALE, L. E., 1965. Biology of the birds of Whero Island, New Zealand, with special reference to the diving petrel and the White-faced Storm Petrel. *Transactions of the Zoology Society of London, 27:* 1–86.

RICKLEFS, R. E., 1973. Patterns of growths in birds. II. Growth rate and mode of development. *Ibis, 115:* 177–201.

SALOMONSEN, F., 1955. The food production of the sea and the annual cycle of Faeroese marine birds. *Oikos, 6:* 92–100.

SCHREIBER, R. W. & ASHMOLE, N. P., 1970. Seabird breeding seasons at Christmas Island, Pacific Ocean. *Ibis, 112:* 363–394.

SERGEANT, D. E., 1951. Ecological relationships of the guillemots *Uria aalge* and *Uria lomvia*. *Proceedings of the International Ornithological Congress X, 1959 (1951):* 578–587.

SMITH, R. I. L. & TALLOWIN, J. R. B., 1980. The distribution and size of King Penguin rookeries on South Georgia. *British Antarctic Survey Bulletin, No. 49:* 259–276.

STONEHOUSE, B., 1960. The King Penguin *Aptenodytes patagonica* of South Georgia. I. Breeding behaviour and development. *Scientific Report of the Falkland Islands Dependencies Survey,* No. *23:* 1–81.

STONEHOUSE, B., 1967. The general biology and thermal balances of penguins. *Advances in Ecological Research, 4:* 131–196.

THORESEN, A. C., 1969. Observations on the breeding behaviour of the diving petrel *Pelecanoides u. urinatrix* (Gmelin). *Notornis, 16:* 241–260.

TICKELL, W. L. N., 1962. The Dove Prion, *Pachyptila desolata* Gmelin. *Scientific Report of the Falkland Islands Dependencies Survey,* No. *33:* 1–55.

TICKELL, W. L. N., 1967. Movements of Black-browed and Grey-headed Albatrosses in the South Atlantic. *Emu, 66:* 357–367.

TICKELL, W. L. N., 1968. The biology of the great albatrosses, *Diomedea exulans* and *Diomeda epomophora*. In O. L. Austin, Jr. (Ed.) *Antarctic Bird Studies, Antarctic Research Series, 12:* 1–55. Washington: American Geophysical Union.

TICKELL, W. L. N. & PINDER, R., 1967. Breeding frequencies in the albatrosses *Diomedea melanophris* and *D. chrysostoma*. *Nature, 213:* 315–6.

WARHAM, J., 1977. Wing loading, wing shapes and flight capabilities of Procellariiformes. *New Zealand Journal of Zoology, 4:* 73–83.

APPENDICES

Appendix 1. Selected measurements of penguins breeding at South Georgia

Species	Body weight (kg)	Flipper area (cm^2)	Culmen length (mm)	Culmen width (mm)	Culmen depth (mm)
King Penguin	15.0	159	133	40	37
Gentoo Penguin	5.8	103	52	43	44
Macaroni Penguin	4.8	78	57	33	39
Rockhopper Penguin	2.5	57	44	27	33
Chinstrap Penguin	4.1	73	49	31	39

All figures are mean values for both sexes combined. Flipper area from Stonehouse (1967). Culmen width and depth measured at base.

Appendix 2. Selected measurements of albatrosses and petrels at South Georgia

Species	Body weight (g)	Wing area (cm^2)	Wing loading ($g\ cm^{-2}$)	Aspect ratio	Buoyancy index	Culmen length (mm)	Culmen width (mm)	Culmen depth (mm)
Wandering Albatross	8727	4337	2.00	15.6	3.2	166	45	63
Black-browed Albatross	3788	2682	1.41	14.9	3.3	117	28	50
Grey-headed Albatross	3788	2389	1.59	15.3	3.1	114	27	44
Light-mantled Sooty Albatross	2840	3226	0.88	–	4.0	110	23	35
Southern Giant Petrel	5165	2748	1.87	–	3.2	95	40	39
Northern Giant Petrel	5212	2846	1.83	11.9	3.0	97	42	40
Cape Pigeon	433	630	0.69	9.2	3.3	31	16	13
Snow Petrel	259	583	0.44	–	3.8	20	10	12
Dove Prion	168	423	0.69	8.5	3.7	30	15	14
Blue Petrel	193	392	0.49	10.8	2.4	27	10	10
White-chinned Petrel	1368	1455	0.94	12.1	3.4	52	21	20
Wilson's Storm Petrel	38	151	0.25	–	3.8	13	8	7
Black-bellied Storm Petrel	53	226	0.23	6.5	4.0	15	8	6
Grey-backed Storm Petrel	29	140	0.24	6.4	3.9	13	5	5
South Georgia Diving Petrel	107	183	0.58	6.9	2.6	15	8	8
Common Diving Petrel	133	174	0.76	7.0	2.5	16	8	10

Body weights and bill measurements are mean values for both sexes combined. Wing areas and aspect ratios from Warham (1977), except for Blue Petrel and South Georgia Diving Petrel. Buoyancy Index is square root of wing area divided by cube root of weight. Culmen width and depth measured at base.